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The Spread of Existing Diurnal Squirrels Across the Bering and Panamanian Land Bridges

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CONTENTS

INTRODUCTION 2
Acknowledgments 3
RELATIONSHIPS ACROSS THE BERING STRAIT AND LAND BRIDGE 3
Assumptions 4
The Four Phyla of the Tribes Sciurini and Marmotini 5
Influences of Pleistocene Continental Glaciation 9
A Fifth Phylum, Tribe Tamiasciurini 11
RELATIONSHIPS ACROSS THE ISTHMUS OF PANAMÁ 12
Direction of Movement 13
The Pygmy Squirrel 14
Species of Intermediate Specialization 14
DISCUSSION 17
Centers of Dispersal 17
Vegetation of the Palearctic Ranges 18
Summary 20
Places of Origin 21
One Possible Hypothetical History 22
SUMMARY 23
LITERATURE CITED 24

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INTRODUCTION

The subfamily of diurnal squirrels, the Sciurinae, constitutes all the squirrel family except the flying squirrels and is thus composed of the tree squirrels, ground squirrels, chucks, chipmunks, giant squirrels, long-nosed squirrels, pygmy squirrels, and ant-eating squirrels. Collectively the Sciurinae may be said at the present time to range naturally and widely over all the continental land masses except Australia. Furthermore, as Darlington (1957) has pointed out, the squirrel family is one of only five families of mammals that do. As a consequence of this nearly cosmopolitan distribution, and also as a consequence of the fact that the animals are diurnal and can easily be collected with a gun, museum material on the Sciurinae should, one might think, provide a good deal of evidence on zoogeographical matters. However, Darlington (1957) found them of little value, particularly because no modern classification of the fossil squirrels exists, but also because the classification of living members of the Sciurinae in 1957 depended somewhat sketchily on characters of the penis bones of the males.

Recently, however, an evaluation of relationships among the 37 living genera within the subfamily Sciurinae (Moore, 1959) has been made possible by discoveries of taxonomic significance in a number of characters of the skull. The most valuable of the skull characters is a simple meristic one of how many bony septa traverse the chamber of the auditory bulla. In some genera there is no transverse septum at all. In many genera there is consistently a single transverse septum. In many others there are two transbullar septa in each auditory bulla, and in still other genera there are consistently three. The number of septa associates many of the genera into the same groups that had already been recognized by characters of the penis bone, and thus supports the earlier classification. Other skull characters were found which further support these relationships and also refine them. As a result, a well-supported classification of the living Sciurinae now exists.

A third line of evidence bearing on the relationships among the genera of Sciurinae has subsequently emerged (Moore, 1961). The number of pairs of functional mammae that characterize a taxon are found to vary from two to six. This third line of evidence in general supports and refines the classification based on the baculum and skull characters.

The virtually cosmopolitan distribution and great diversity of the subfamily Sciurinae, and the strength that has accrued to our knowledge of the relationships among its component parts, now seem to make it not only possible but necessary for one to try to explain the existing geography of the subfamily. The present paper seeks to give such an explanation

for the Holarctic and Neotropical members now living, without attempting to assess how the poorly understood fossil record bears on the various problems.

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RELATIONSHIPS ACROSS THE BERING STRAIT AND LAND BRIDGE

The oldest known fossil of a squirrel is from the Palearctic Region, and, as the Nearctic Region has been better searched for Tertiary mammals, it seems a fair inference for the time being that squirrels first crossed eastward from the Palearctic Region to the Nearctic. If one counts the number of species of squirrels in the four living Holarctic subtribes of Sciurinae to determine on which side of Bering Strait the greatest number of species occurs, one easily infers that a considerable radiation has taken place in North America, and that at least one species each of these four subtribes must have spread back across the Bering land bridge to the Palearctic Region as a result of the radiation in the Nearctic.

Simpson (1947), in his study of the Cenozoic history of the Bering land bridge, found more evidence of the spreading of mammals eastward across the bridge than westward. Darlington (1957, p. 561), in his general zoogeography, reports that eastward spreadings across the Bering land bridge appear to outnumber westward ones in each of the classes of vertebrates. This greater movement to the east supports Mathew's (1915, 1939) concept of the Palearctic as the historical world center of the dispersal of vertebrates and also Darlington's (1957, 1959) concept of the Old World tropics as the main dispersal center.

Nevertheless, as shown in table 1, the number of species of diurnal

squirrels on the Nearctic side is much greater than that on the Palearctic side. This imbalance in number of species creates the impression that diurnal squirrels must have radiated adaptively in the Nearctic Region and eventually spilled over into the Palearctic Region by *westward* spread across a Bering land bridge. Because such an interpretation is contrary to the general trend reported by Simpson and Darlington, some reëx-

TABLE 1
DIURNAL SQUIRRELS THAT SPAN THE BERING STRAIT
(Numbers of species are those accepted by Ellerman and Morrison-Scott, 1951, and Hall and Kelson, 1959.)

Palearctic Region	[Bering Strait]	Nearctic Region
Tribe Marmotini		Tribe Marmotini
Subtribe Spermophilina		Subtribe Spermophilina
Spermophilus undulatus and six other species		*Spermophilus undulatus,* 22 other species, *Ammospermophilus,* and *Cynomys*
Subtribe Marmotina		Subtribe Marmotina
Marmota marmota, M. himalayana, and *M. caudata*		*Marmota caligata* and four other species
Subtribe Tamiina		Subtribe Tamiina
Eutamias sibiricus		*Eutamias minimus,* 15 other species, and *Tamias*
Tribe Sciurini		Tribe Sciurini
Subtribe Sciurina		Subtribe Sciurina
Sciurus vulgaris and *S. (Tenes) anomalus*		*Sciurus carolinensis* and 13 other species
Tribe Tamiasciurini		Tribe Tamiasciurini
Sciurotamias davidanus and *S. (Repestes) forresti*		*Tamiasciurus hudsonicus* and *T. douglassi*

amination of the evidence on squirrels may be in order. It is true that, whereas Ellerman and Morrison-Scott (1951) carefully lumped some Palearctic species, Hall and Kelson (1959) carefully did not do so with the Nearctic ones. A comparison of the number of species in their lists may thus involve some error, but the Nearctic squirrels have been better collected and are better understood at the specific level than are Palearctic ones, so that such an error contributes very little to the differences shown in table 1. The apparent incongruity of the (major) direction of spread of diurnal squirrels may be examined here.

ASSUMPTIONS

In seeking to determine which way each of the present Holarctic phyla of Sciurinae has most recently spread, one may conveniently make three assumptions: First, it is assumed that the principle voiced by Darlington (1957, p. 553), that "It is the dominant groups which spread," applies at

the specific level. Second, it is assumed that, when other things are equal, a relatively greater area of range for a species provides a relatively larger population in which more mutations can be tried. Third, it is assumed that, when other things are equal, the possession of a much larger range will keep a species ahead of closely related species (i.e., most probable competitors) in the evolution of characteristics that are advantageous in the exploitation of the species niche. For this discussion, therefore, among closely related species the occupation of a greatly larger range is accepted as presumptive evidence of dominance.

The four major ecological niches occupied by diurnal Holarctic squirrels (niches of ground squirrels, giant ground squirrels, chipmunks, and tree squirrels) differ from one another so greatly that species occupying one niche do not evidently compete with species occupying another. In theory, then, there can be in the Holarctic Region a dominant species in each of these four niches. The several species occupying each of these four niches have been shown to be at least subtribally distinct (Moore, 1959). If one can certainly determine which (if any) species is dominant in one of these subtribes, it will be consonant with our assumption stated above to infer that the latest spreading across the Bering land bridge by that subtribe was in the direction away from the present range of the dominant species.

The Four Phyla of the Tribes Sciurini and Marmotini

The range of the subtribe Spermophilina is substantially more extensive in the Palearctic Region than in the Nearctic (Moore, 1959, fig. 7). However, in the Palearctic only seven species are recognized by Ellerman and Morrison-Scott (1951), whereas 22 are recognized in the much smaller Nearctic subtribal range by Hall and Kelson (1959). The ground-squirrel species nearest Bering Strait, *Spermophilus undulatus,* possesses the largest geographic range. The Palearctic part of its range extends more than 3000 miles from Bering Strait to between Lake Zaisan and Lake Balkhash, at the center of the Eurasian continent. It embraces the Okhotsk Sea on the southeast and extends north of the Arctic Circle from the Lena River to Bering Strait. *Spermophilus undulatus* also possess a very large range in North America, covering virtually all Alaska ar extending eastward to Hudson Bay. The extension into the Nearc Region is cut off from the main range of the species and is consequen not here considered a functional part of the size of its range as a do nant species. The Palearctic portion of its range alone is large eno however, to indicate the status of *undulatus* as the dominant ground-sq rel species. The Nearctic population of *undulatus* may, if the barrier

Bering Strait keeps it separated from the Palearctic population long enough, in time evolve beyond the point of sexual isolation. As Gilmore (1946) suggests, the Palearctic population probably spread to a limited unglaciated area eastward across the Bering land bridge during the latest glacial period and later, following the glacial retreat, expanded farther.

The second subtribe, the giant ground squirrels (Marmotina), has a distribution (Ognev, 1947, p. 240, map 6; van den Brink, 1955, p. 83; Hall and Kelson, 1959) very similar to that of the ground squirrels (Spermophilina). Ellerman and Morrison-Scott (1951) were apparently justified in lumping some previously accepted Palearctic species of *Marmota,* but they appear to have stopped short of a tenable position by admitting *bobak* to the status of species. *Marmota bobak,* as a species recognized by Ellerman and Morrison-Scott and judged from Ognev's above-cited map, interposes a barrier about 1000 miles wide between *Marmota marmota marmota* of Europe and *Marmota marmota baibacina* of middle Asia. *Marmota m. baibacina* in turn separates *M. bobak bobak* from *M. bobak sibirica. Marmota b. sibirica* in its turn separates *M. m. baibacina* from *M. m. camschatica.* These five forms of *Marmota* are thus distributed in an essentially linear fashion west to east across the Palearctic Region, with numbers 1, 3, and 5 alleged to be of one species and numbers 2 and 4 of another. However, it is unnecessary to tax one's credulity with such an unlikely arrangement, for Ellerman and Morrison-Scott (1951, p. 513) state that *M. marmota* and *M. bobak* "tend to grade into each other in our material." As Ellerman and Morrison-Scott separated *M. marmota* and *M. bobak* only on the length and thickness of the pelage and note a tendency towards intergradation, it seems an acceptable if not necessary procedure to treat the several subspecies of *bobak* as subspecies of *M. marmota.* This arrangement would recognize, for the single species *Marmota marmota,* a vast range extending from the Pyrenees to the Bering Sea, although broken at least by two gaps without marmots in western Europe and one area without marmots north of Lake Balkhash. The species *M. caudata* and *M. himalayana* would then be restricted to middle Asia south of the range of *M. marmota.*

In the Nearctic Region the woodchuck species *Marmota monax* has a large, continent-wide range. One of the two other species of giant ground squirrel with large ranges in the Nearctic Region, *Marmota caligata,* is restricted to the northwest, partly sympatric with both *monax* and the more southwestern species *flaviventris.* No impressive difference appears to exist between the two Holarctic regions in the number of species of *Marmota.* If *Marmota marmota* is the dominant species of the subtribe, as

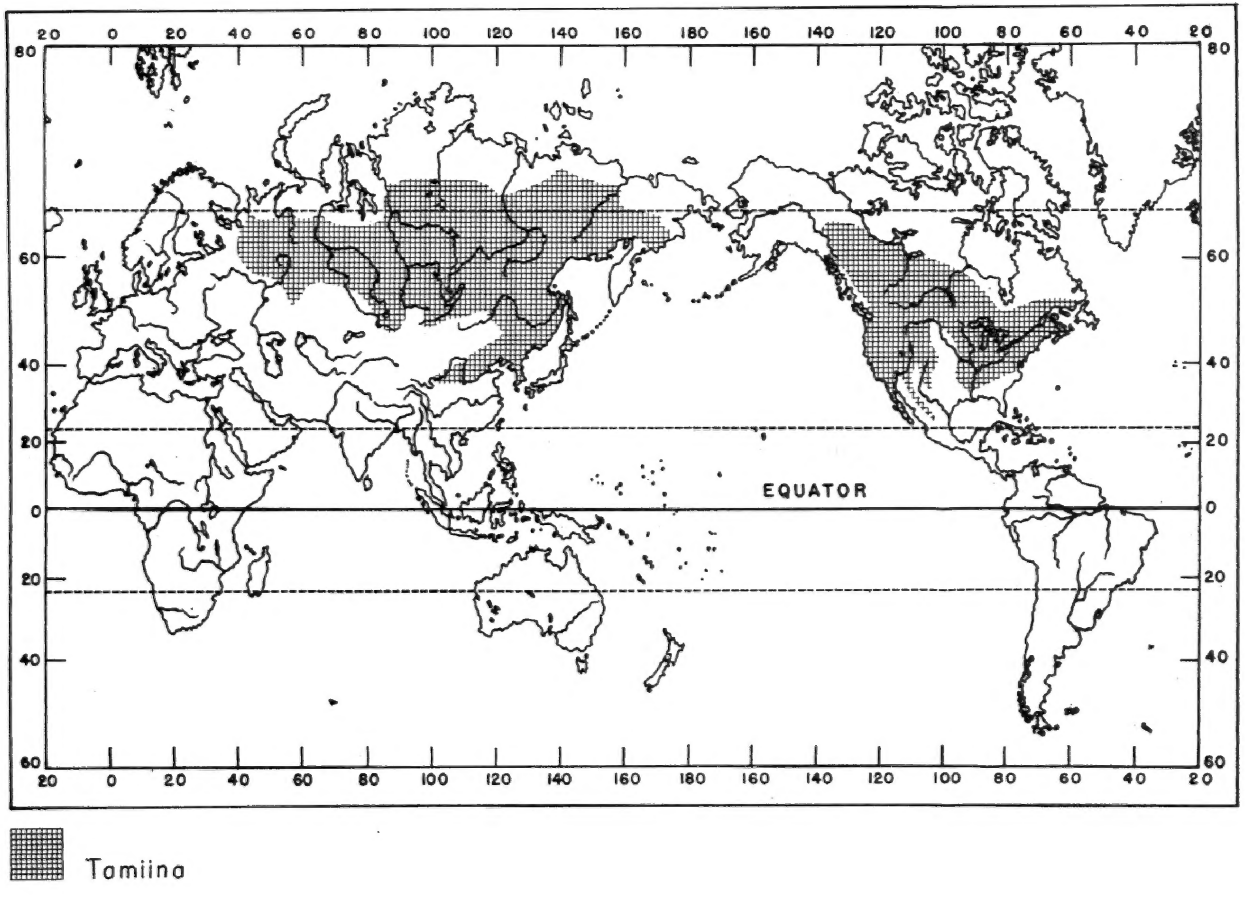

FIG. 1. The range of the Holarctic subtribe Tamiina (chipmunks).

can only be conjectured here, it could be construed to have spread eastward successfully at least three times across the Bering land bridge, each time leaving an isolated population in the Nearctic Region which has speciated and survived.

Of the third subtribe, the chipmunk subtribe Tamiina, only one species is recognized in the Palearctic Region, and that one possesses a range which extends 4000 miles from the White Sea to the Bering Sea and the Yellow Sea. In the Nearctic Region there are 16 species of chipmunks (Hall and Kelson, 1959) in two genera. Figure 1 shows the range of the Tamiina. On a globe the range of the single Palearctic species, *Eutamias sibiricus,* appears to be about as large as the combined ranges of the 16 Nearctic species. This Palearctic species of chipmunk certainly appears to be in possession of a range indicating dominance over other chipmunk species, and has doubtless made contributions to the numerous species of Nearctic chipmunks by invasion at intervals across a Bering land bridge.

Figure 2 shows the range of the fourth subtribe, the tree-squirrel subtribe Sciurina, the Palearctic part of which, except for the discrete range of *Tenes* in Asia Minor, is constituted wholly by the enormous range of a single species, *Sciurus vulgaris,* which extends over 6000 miles from Spain to the Bering Sea. This extraordinary range of a single species provides the largest continuous interbreeding population of tree squirrels in the world. The lack of any other tree-squirrel species sympatric with, or even in geographic contact with, *Sciurus vulgaris* suggests that any other species that may have been in such contact failed to survive the competition. So large a range without competitors may perhaps be said to epitomize that of a dominant species.

Compared on a globe, the ranges of the dozen or so species of the tree squirrels of the Nearctic Region combined are much smaller than the range of the single Palearctic species *S. vulgaris.* As is detailed below, the vast boreal coniferous forest of the Palearctic Region and its two great areas of mixed deciduous forest are all occupied by the single species *S. vulgaris.* But in North America (Hall and Kelson, 1959) the one great mixed deciduous forest is inhabited by two species of tree squirrels, the ranges of both of which approximate the extent of the forest; a third species occupies the contiguous boreal coniferous forest alone. The interpretation of *Sciurus vulgaris* as a dominant species suggests that as such it must have contributed at least one species, and doubtless a succession of several species, to the Nearctic Region by widely separate, successful invasions eastward across a Bering land bridge. For example, the most recent such invasion might have left a population that has sub-

sequently evolved to form the species of gray squirrel named *Sciurus carolinensis;* another may have left a population that has evolved to constitute the fox-squirrel species *Sciurus niger.*

Influences of Pleistocene Continental Glaciation

A question may arise as to whether or not the above-mentioned four distributions of subtribes of Holarctic squirrels can be interpreted as westward migrations from a Nearctic center of distribution across a Bering land bridge into an unoccupied area freshly vacated by the latest Pleistocene continental glaciers. The tree squirrel *Sciurus vulgaris* now occupies Spain, Italy, and Greece which surely would have been adequate refugia for it during the latest continental glaciation (Moreau, 1955, pp. 270, 271), and from which the refugees could be expected to have sallied forth as fast as forests followed behind the retreating ice sheet. The giant ground squirrel *Marmota* now occupies a range on the southern slope of the Alps in Europe and the southern slopes of the Himalayas in northern India, where it might quite well have survived the continental glaciation. Ground squirrels of the genus *Spermophilus* now range south well across Asia Minor, which could have served them as a refugium during the latest glaciation. *Eutamias sibiricus* now ranges southeast into the northeastern provinces of China, which certainly could have served it as a refugium during the latest glaciation (Flint, 1957, pl. 3). Thus each of these squirrel subtribes would have reoccupied more quickly the glaciated areas of the Palearctic Region from these southern refugia by moving with suitable vegetation northward behind the melting glaciers than by moving eastward with suitable vegetation across the far more northern Bering land bridge.

There is evidence (Hopkins, 1959, p. 1524) of successive periods during the Pleistocene when the sea alternately intruded a strait and bared a land bridge between Siberia and Alaska. Hopkins (1959, p. 1527) considered the evidence good, however, that (1) during the latest period of land connection, and (2) perhaps during some earlier Pleistocene periods of land connection, and (3) possibly during all the Pleistocene periods of land connection, the land bridge was covered by tundra but no trees. The tree squirrels could not have crossed at any time during the emergence of a land bridge when forest did not spread onto the bridge, although the other squirrels could. One would therefore expect the ground squirrels and giant ground squirrels existing on opposite sides of Bering Strait at the present time to be more closely related to each other than the tree squirrels are to each other. The chipmunks, which seem to require at least scrubby trees, might be expected to exhibit a stage of dif-

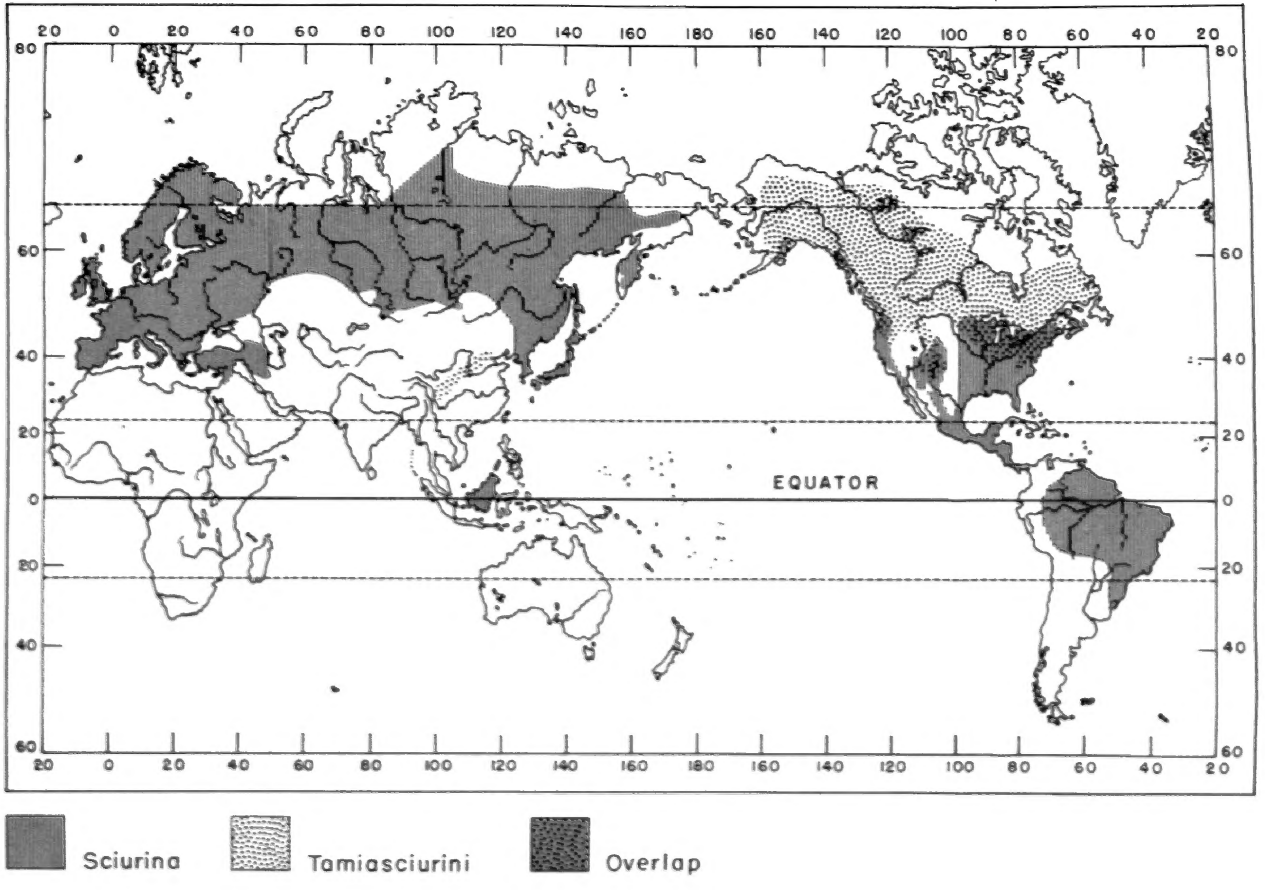

FIG. 2. The ranges of the tree squirrels, subtribe Sciurina and tribe Tamiasciurini.

ferentiation intermediate between the stages of differentiation revealed by the giant ground squirrels and the tree squirrels. What one finds is this: The ground squirrels that now straddle the Strait are quite generally accepted as a single species, *Spermophilus undulatus*. The giant ground squirrels that occur on elevations on each side of the Strait are considered both by Ellerman and Morrison-Scott (1951, p. 513) and by Rausch (1953, p. 117) to belong to a single species, although the population of giant ground squirrels on the Alaskan side is provisionally retained as a distinct species, *Marmota caligata,* by Hall and Kelson (1959, p. 327). The chipmunks occur at some distance from the Strait on each side. They are unquestionably two good species, *Eutamias sibiricus* and *Eutamias minimus,* and in fact are ranked as subgenera by White (1953), although it must be said that in my experience with the subfamily as a whole, these subgenera are extremely weak. Finally, the tree squirrels, excluding *Tamiasciurus* which is discussed below, are separated at present by a gap of more than 2500 miles and are the definitely distinct species *Sciurus vulgaris* and *S. carolinensis*. (These two have long been regarded as differentiated at the subgeneric level, but without substantial basis, and elsewhere the present writer repudiates this subgeneric distinction.)

A Fifth Phylum, Tribe Tamiasciurini

The tree-squirrel niche of the boreal forests of the Nearctic Region is occupied by the chickaree, *Tamiasciurus,* which is distinct on a tribal level from *Sciurus*. The distribution of this squirrel throughout boreal forested North America (fig. 2) constitutes strong additional evidence on the question of whether the most recent crossing by tree squirrels has been eastward or westward. When westward spreading across the land bridge was most recently possible for tree squirrels, the chickaree should have been the most competent to cross and the first to have the opportunity. For evidence as to whether it did spread across one may look for relatives of it in Asia. The closest living relative of the chickaree is presumed to be the rock squirrel of China, *Sciurotamias davidianus* (fig. 2), from which it shows, however, exceedingly strong generic distinction. If such close relationship is offered as evidence of the early westward crossing of the land bridge by ancestors of the chickaree, it must also be offered as evidence that the crossing was made very long ago, possibly in the early Pliocene or earlier. The ecological niches of these two genera are not even equivalent, and it would be rash to rely on the relative sizes of their ranges, after so long a time and such morphological differentiation, to indicate which way the migration moved.

While the chickaree (*Tamiasciurus*) possesses a range that may be said

to characterize it as the dominant tree squirrel in the Nearctic Region, *Tamiasciurus hudsonicus* is obviously only second in dominance to *Sciurus vulgaris* in the Holarctic regions as a whole. When spreading across a Bering isthmus was possible, *Tamiasciurus* must surely have succumbed where it came into competition with *S. vulgaris*. Perhaps the invading population of *Sciurus vulgaris* in such instances soon became isolated from the Palearctic, but, if spread were rapid, then the more they expanded from their bridgehead, the more inbred and provincialized they would have become. The reason for such provincialization is that the gene pool of the spreading colony would have been drawn more rapidly from the small original stock that had spread across than siphoned across the tenuous land bridge from the enormous Palearctic population. Perhaps the provincialization of the invaders reached a magnitude, after isolation from Asia became complete, that enabled *Tamiasciurus* to assert dominance over the newcomers and to replace them in the northern Nearctic coniferous forests. If the Bering land bridge remained unsuitable for tree squirrels for a long enough time, *Tamiasciurus* would cause the extinction of any of the population of new invaders which did not spread southward out of the northern coniferous forest.

In summary, if the basic assumptions are correct, it is possible to state with some confidence that the two phyla (Sciurina and Tamiina) that appear most likely to have spread west have most certainly spread east; and that successive, widely spaced, eastward crossings may have produced a number of the existing species of the Sciurinae, and thus exaggerate the indications of a radiation of diurnal squirrels in North America.

RELATIONSHIPS ACROSS THE ISTHMUS OF PANAMÁ

The Isthmus of Panamá is the land bridge that emerged and connected the two American continents quite a short time ago geologically—about Blancan time, according to Simpson (1950, p. 381). Blancan is accepted as transitional between Pliocene and Pleistocene (Hibbard, 1958, p. 8). The two continents of the Western Hemisphere had previously been separated by seaways for a very much longer time than they have since been connected. The separation was continuous, according to Simpson (1950, p. 373), as far back as the late Cretaceous-Paleocene, at which time he considers there is evidence that an early connection existed, although Woodring's (1954, p. 724) map of Middle America for the late Cretaceous gives little encouragement for the concept of a land bridge even then.

The Isthmus of Panamá is, of course, somewhat distant from the hypo-

thetical line that now separates the Nearctic Region from the Neotropical Region (Darlington, 1957, p. 457). In the distribution of the squirrel fauna as known at the present time, however, the Isthmus of Panamá makes a moderately good break between the Neotropical and the Nearctic genera. The Neotropical genera *Syntheosciurus* (which includes the species *granatensis* in the subgenus *Mesosciurus,* according to the present author's revision, 1959, pp. 179, 199) and *Microsciurus* both penetrate a short distance into Central America north of the Isthmus of Panamá (see Hall and Kelson, 1959, maps, pp. 394, 396–398). The Holarctic genus *Sciurus* (as revised by the present writer, 1959, p. 177) does not cross the Isthmus of Panamá into South America. The species of *Sciurus* that ranges closest to South America, as judged from the distribution maps in Hall and Kelson (1959, p. 381), is *Sciurus variegatoides,* a species with a known range that extends less than 50 miles across the Panamá Canal. The range of the pygmy-squirrel genus *Sciurillus* of South America, as known at the present time, approaches the Isthmus no closer than some hundreds of miles, and the genus *Guerlinguetus,* as redefined by Moore (1959, p. 177), also remains somewhat remote from it.

The squirrel fauna involved in the relationships across the Isthmus of Panamá is simpler than that of the Bering Strait, being constituted entirely of one tribe instead of three. The tribe Sciurini is the only one known to have reached the Isthmus of Panamá, the other tribes represented in the Nearctic Region having apparently failed to reach the Neotropical Region (Tamiasciurini), or to penetrate more than the very margin (Marmotini) of it. That a single tribe has crossed the Isthmus of Panamá is well established by the characteristics of the baculum (os penis) of *Sciurus* type in all the South American forms for which the baculum is known (Anthony and Tate, 1936; Didier, 1952, 1955; see also table 2).

Direction of Movement

There is no evidence that squirrels occurred in South America before the very late Pliocene (Simpson, 1950), but fossil squirrels are known from many earlier North American horizons (Bryant, 1945, p. 339), as far back at least as the lower Miocene. This condition and the established morphological relationships among the living forms provide basis enough for an inference that the South American squirrels came (via Central America) from North America. Our knowledge of the ranges of the species of Neotropical squirrels is entirely inadequate for an analysis of the kind applied in the case of Bering Strait.

The Pygmy Squirrel

Isolation of the South American continent for virtually the entire Tertiary protected it from invasion by many phyla of evolving mammals until the very late Pliocene. As Wood (1959, p. 359) considers the Sciuridae to have evolved in the middle or lower Oligocene, it is assumed that no fossil squirrels have been found in South America of an age earlier than the emergence of the Isthmus of Panamá, because none chanced to reach South America earlier. However, *Sciurillus,* the pygmy squirrel of South America, which is shown (Moore, 1961) to be distinguishable from all other diurnal squirrels in the world by at least six skull characters, is too highly differentiated a genus to have evolved during the geologically very short time that squirrels have evidently lived in South America. The possibility of a much earlier arrival of *Sciurillus* in South America has been considered earlier by the present writer (1959, p. 191) and rejected. Pygmy squirrels are shown (in the same paper) to be a purely tropical adaptation among living squirrels, each major tropical land mass of the world having one or two endemic equatorial genera which have evidently evolved from local stock. It has seemed necessary to postulate that the South American genus, *Sciurillus,* evolved during a period geologically much longer than the Pleistocene, either on the tropical southern tip of the North American continent or, more likely, on a generous portion of Central America isolated from North America.

The original attainment of *Sciurillus* to the pygmy condition is regarded not as the result of dwarfing from genetic processes attendant on long isolation as a reduced population on a small island free of other squirrels. In order to have survived the subsequent competition of other squirrels on a large continent, the South American pygmy squirrel, perhaps after an initial isolation long enough for it to speciate, more likely evolved towards the pygmy condition and presumably specialized habits in the presence of probably more than one other species of squirrels for perhaps several millions of years.

Species of Intermediate Specialization

Other squirrel species that may have evolved in the tropical Central American habitat with *Sciurillus* and that have become adapted to niches requiring or permitting less morphological specialization may also have survived. In looking for the species most likely to be such survivors (see table 2), one may note several lines of evidence that point to the subtribe Microsciurina. Morphologically, the low squamosal, which is so important as to distinguish the subtribe Sciurina from all other diurnal squir-

rels, strongly associates the South American genus *Guerlinguetus* with Holarctic *Sciurus* in the same subtribe. The Microsciurina constitute a purely Neotropical subtribe characterized by high squamosals. Geographically, the occurrence of *Syntheosciurus* (*S.*) *brochus* and *S.* (*S.*) *poasensis* as endemic relicts in the Cordillera of lower Central America (see Hall and Kelson, 1959, map, p. 396) strongly suggests origin or early establishment there. (An earlier arrival on a mountainous island, if it survives the invasion of a more successful competing species arriving later by a newly emerged land bridge, is more likely to survive at the higher elevations than at the lower.) Likewise, the present occupation by *Microsciurus* (*M.*)

TABLE 2

SQUIRRELS IN RELATION TO THE ISTHMUS OF PANAMÁ

North and Central America	[Isthmus of Panamá]	South America
Subtribe Sciurina		Subtribe Sciurina
Sciurus variegatoides and seven other tropical species		*Guerlinguetus aestuans, G. ingrami, G.* (*Hadrosciurus*) species
Subtribe Microsciurina		Subtribe Microsciurina
Syntheosciurus brochus, S. poasensis, and *S.* (*Mesosciurus*) *granatensis*		*Syntheosciurus* (*Mesosciurus*) *granatensis*
Microsciurus alfari and *M. boquetensis*		*Microsciurus* species, *M.* (*Leptosciurus*) species, and *M.* (*Simosciurus*) *stramineus*
		Subtribe Sciurillina
		Sciurillus pusillus

and *Microsciurus* (*Simosciurus*) of the western face of the Andes, while *Guerlinguetus* inhabits the lowlands of the Amazon basin, suggests an earlier arrival in South America of the phylum that now constitutes the Microsciurina. The phylum that now constitutes *Guerlinguetus* may have spread into South America much later in the Pleistocene.

The *Guerlinguetus* phylum probably spread into South America as a single dominant species of generalized tree squirrel successfully competing with and replacing any generalized tree-squirrel species of the Microsciurina resident in the lowlands. It may since have speciated several times, and no doubt its smaller species have tended to compete with and replace the small forms of *Microsciurus* and *Syntheosciurus* wherever they came in contact in eastern South America and eliminated the subtribe Microsciurina from the Amazon basin and other eastern parts of South America. *Guerlinguetus* presumably has evolved no species small enough to compete successfully for the ecological niche of *Sciurillus* which still occurs in the Guianas and the Amazon basin. Subsequent to this putative invasion by the phylum of *Guerlinguetus,* the species *Syntheosciurus* (*Mesosciurus*) *granatensis* evidently expanded its range at the expense

of *Guerlinguetus* in the northern part of South America adjacent to Central America (see Allen, 1915, range maps, pp. 298–301).

The subtribe Microsciurina is well represented in Central America. The three principal species that represent it there, *Microsciurus alfari, Syntheosciurus brochus* (with which *S. poasensis* may prove synonymous), and *S. (Mesosciurus) granatensis,* appear to have coinciding northern limits in Costa Rica (Hall and Kelson, 1959, maps, pp. 394, 396, 397) just south of what may have been a seaway across Nicaragua marking the northwestern end of one former Central American island that includes what is now Costa Rica and northern Panamá. The ranges of the Microsciurina extend from Panamá into South America, principally along the western slopes of the Andes (J. A. Allen, 1915, maps, pp. 298–301), the nearer part of which Hershkovitz (1958, map, p. 586) considers to belong zoogeographically with Panamá and Costa Rica in the Middle American Province.

Central America, in addition to its important role as a filter barrier that prevents the passage of those mammals not adapted to its ecology and as a pathway for occasional, ecologically adapted "island hoppers" that accidentally crossed the seaways (Simpson, 1950, p. 387), appears to have served as a prolonged "staging area," at least for part of the existing squirrel fauna of South America. By reaching Central America, as waifs or by temporary land bridges, such squirrels speciated and developed adaptations to tropical conditions and to one another, in (perhaps intermittent) isolation for a substantial period of time, before the emergence of the Panamanian isthmus opened the way for a direct invasion of South America.

The concept of Central America as an island, or a series of islands, during the Miocene and Pliocene that served as a "staging area" in which mammals of Nearctic origin speciated and became thoroughly adapted to, and differentiated in, tropical conditions before the emergence of the Panamanian land bridge is not new. Simpson (1950, p. 388) says: "It is an obvious fact . . . that the immigrants from North to South America did not come from the continent as a whole . . . but only from Central America. . . . Thus Central America must have had a fauna mainly or purely North American in origin . . . and been an important center of regional differentiation. . . . This special local fauna was the one, and the only one, available for spread into South America." But he concludes, "details have not yet been adequately studied, if at all, from this point of view." Earlier Simpson (1943) and Dunn (1931) presented herpetological evidence of the role of Central America as a "staging area." The present offering is apparently the first to give detailed evidence of this role of staging area for a mammalian family.

DISCUSSION

It is observed that living representatives of four phyla of diurnal squirrels are represented on both sides of Bering Strait by taxa that can be differentiated at lower than the rank of genus. In each of the subtribes Spermophilina, Marmotina, Tamiina, and Sciurina, the species that possesses the greatest geographic range is on the Palearctic side of the Strait. In each of the four subtribes the numerical superiority of species is on the Nearctic side. In three (the Marmotina, the Tamiina, and the Sciurina), the geographic range of the paramount Palearctic species approximates or exceeds in area the total single range of all the Nearctic species in its respective subtribe.

In all four subtribes, the number of species in the Nearctic Region suggests that an adaptive radiation has taken place (Spermophilina, 33; Marmotina, 5; Tamiina, 17; Sciurina, 14). But the number of species in the Palearctic Region (Spermophilina, 7; Marmotina, 3; Tamiina, 1; Sciurina, 2) suggests an adaptive radiation in only one phylum. These data would appear to imply (erroneously, I think) that by far the greater adaptive radiation of the existing tribes Marmotini and Sciurini took place east of Bering Strait and that the Palearctic distribution resulted from a successful *westward* spreading across a Bering land bridge during the Pleistocene.

Centers of Dispersal

It is accepted as applicable here that, other things being equal, a species with a much larger geographic range and thus a much larger total population can try enough more mutations to give it an advantage over closely related species in adaptation to the same niche or closely similar niches. It is also accepted that species with much larger geographic ranges, possessing such an advantage, are the ones that spread. The applicability of the competitive-exclusion principle here is accepted. Thus, in most cases, when spreading brings about the overlapping of the ranges of two closely related species, the one with the much larger range may be supposed to succeed in competition with the other and to replace it. The successful species is then recognized as the "dominant" species of the two in this connection, much as Darlington (1957) uses the term "dominant" for successful taxa of much higher rank.

It is shown in the present paper that, in each of the four subtribes of diurnal squirrels that are represented on opposite sides of Bering Strait by taxa that can be differentiated at a level lower than that of genus, there is one Palearctic species with so preponderantly large a species range that it must be regarded as the dominant or potentially dominant

species of its phylum. It is the one that should succeed at the expense of any other member of the phylum with which it might come into competition. Under these conditions the emergence of a Bering land bridge and the establishment of habitat conditions over it suitable to support a population of any of these four subtribes would permit a spreading across it only eastward.

Confronting each other across Bering Strait, also, are two species that differ not only at the generic but at the tribal level. They, nevertheless, replace each other ecologically, each as the only tree squirrel of the boreal forest in its region, and they would surely compete if brought together. These two species are *Sciurus vulgaris* of the tribe Sciurini on the Palearctic side and *Tamiasciurus hudsonicus* of the tribe Tamiasciurini on the Nearctic. The theoretical considerations applied to two species of the same genus would be more doubtfully invoked, but, by whatever chance, their applicability does appear to be supported by the evidence of present distribution. That is, for this pair of species, also, all evidence of recent spreadings across a Bering land bridge indicates spreading to the east.

It is true that the evidence that is offered of the occurrence of much larger specific ranges on the Palearctic side of Bering Strait is all contemporary. However, the physical conditions of the area in which the large specific ranges occur may have existed continuously for a large part of the Cenozoic: Eurasia was the largest of continental land masses; a suitable climate, which was interrupted during the Pleistocene by glaciations, but was generally even more favorable during the latter part of the Tertiary than now; and the probable lack of effective and long-persisting barriers to dispersal within the continent. Thus the conditions that appear at the present time to promote the eastward dispersal from west to east across the Bering land bridge may reasonably have existed or recurred persistently even as far back as the origin of the family, which seems to have been in the middle Oligocene (Wood, 1959, fig. 2). For the areas and phyla considered in the present paper, and in view of the assumptions that are made, the Palearctic Region is quite evidently the center of dispersal, both early and late.

Vegetation of the Palearctic Ranges

The general character of the vegetation of this "great Palearctic species range" has been sketched by Moreau (1955, p. 256), and a comparison of his map with maps for the squirrel species by van den Brink (1955, map 75) and Ognev (1940, p. 342) reveals that there are three major vegetation types across the northern Palearctic Region with which

the range of *Sciurus vulgaris* rather nicely coincides. These are from east to west: (1) a mountainous zone of mixed types constituting about one-quarter of the range of the squirrel; (2) the taiga, constituting about one-half; and (3) deciduous forest, constituting about one-quarter. The Oriental area of deciduous forest on the mainland from the Korean Peninsula and Peking north and on Japan is also included in the range of this squirrel. South of the western half of the taiga there is also a broad band of wooded steppe from about longitude 30° E. to longitude 90° E., and a still smaller area of Mediterranean vegetation on the Iberian, Italian, and Balkan peninsulas is also within the range.

It is notable that the range of the chipmunk (Ognev, 1940) is very nearly the same as the eastern three-fifths of the range of the tree squirrel. The range of the chipmunk very curiously stops in the taiga east of longitude 40° E. and thus does not reach the deciduous forest of Europe. The chipmunk seems to stay out of the band of wooded steppe except at the very eastern end and where the taiga penetrates it. The chipmunk does, however, range throughout the eastern deciduous forest area which embraces the Yellow Sea and westward well into the steppe area of the Yellow River country.

Ognev's (1947, pp. 24, 52) map of the range of *Sphermophilus undulatus* shows that this ground squirrel occupies the mountainous area of eastern Siberia and also the tundra east of the mountains and north of them to latitude 70° N. in several places. This species does not penetrate much of the main taiga area sketched by Moreau (1955, p. 256) but remains chiefly east or south of it, except in the basin of the three main forks of the Lena River and a small triangle immediately west of Lake Baikal. Thus *undulatus* in Asia inhabits principally the "mountainous zone" containing all vegetation types (but in which it would surely occupy alpine habitats similar to tundra). This "mountainous zone" is the only one of the major vegetation areas employed by Moreau that *undulatus* exploits rather fully. Other vegetation zones that this species has spread well into, although it has occupied less than half of the continuous area apparently available to it, are tundra, mixed taiga and woodland, taiga, and steppe. Compared with the ranges of *Sciurus vulgaris* and *Eutamias sibericus,* therefore, in adaptation to habitats within major Palearctic vegetation types, the range of *Spermophilus undulatus* is notably more restricted and shows in this respect less indication of dominance. Ognev (1947, maps 1, 2) shows that the range of *S. undulatus eversmanni* overlaps the ranges of *S. pygmaeus brevicauda* and *S. major erythrogenys* near Lake Zaisan (the name combinations from Ellerman and Morrison-Scott, 1951).

The range of the subtribe Spermophilina as a whole across the Pale-

arctic Region remains in the steppe, mountainous zones, wooded steppe, semi-desert, and desert, but penetrates the mixed deciduous forest at the European end, principally in the Danube Valley (following man-made clearings?). Thus the range of the Spermophilina has a large eastern area of coincidence with the ranges of both the dominant tree-squirrel and chipmunk species, but west of a line from Lake Baikal northeast to the mouth of the Yana River, it lies south of the ranges of both *Sciurus vulgaris* and *Eutamias sibiricus*.

Ognev's (1947, pp. 235, 240) maps of the range of *Marmota* show sporadic distribution in the large mountainous zone of the eastern end of the Palearctic Region and north of it in the tundra about the mouths of the Lena and three other rivers to the east. It does not range into the Oriental deciduous forest, but the form *sibiricus* is shown to enter the northern edge of the steppe near the headwaters of the Amur. Nor does it range into the taiga, aside from some distribution near the Lena and Aldana rivers at about latitude 60° N. and one spot on the Arctic Circle at longitude 105° E. From Lake Zaisan west to the Black Sea *Marmota* seems restricted to, but well distributed in, the wooded steppe, except that there is a curious gap from longitude 70° E. to longitude 80° E. In Europe it is restricted to three small, disjunct, montane areas. The Palearctic range of the subtribe Marmotina coincides therefore with that of the Spermophilina very closely, except for being somewhat more restricted (extending very slightly into the steppe and not at all into the semi-desert and desert). A curious zoogeographic difference that becomes apparent here is that *Spermophilus* is distributed westward across the Chinese steppe into Kansu towards the eastern face of the high Tibetan Plateau, but the species of *Marmota* that are on that face appear, from the presently known distribution, to have attained it by spreading from the Tien Shan south to Kashmir and east through Tibet or along the southern face of the Himalayas (Glover M. Allen, 1940, p. 713; Ellerman and Morrison-Scott, 1951, p. 515; and Ognev, 1947, p. 240, but without a map of the range of *himalayana*).

SUMMARY: It is now evident that for diurnal squirrels the potentially enormous range for a single species in the northern Palearctic Region varies a little geographically for different phyla, as one might expect, but is very closely sympatric for two ground-squirrel phyla, the Marmotina and the Spermophilina, and is surprisingly sympatric as well for another ground-squirrel phylum, the Tamiina, and the tree-squirrel phylum, the Sciurina. Although not amounting to allopatry, a substantial geographic difference shows up between the sympatric ranges of one pair of phyla and the sympatric ranges of the other pair. Vast areas of the

taiga and of the deciduous forest are included exclusively in the combined ranges of the tree squirrel and chipmunk species. Vast areas of tundra, steppe, and semi-desert are included exclusively in the combined ranges of the subtribes of the ground squirrels and giant ground squirrels. Wooded steppe and mountainous zones (containing all vegetation types) are common grounds.

Places of Origin

The places of origin that are possible for the Holarctic phyla of Sciurinae may be conjectured from the manner in which dispersal from the Palearctic center must have worked. The first species to occupy a Palearctic niche, adaptation to which would make it ancestral to all presently living Holarctic Sciurinae, may have originated by the spread of an already successful squirrel species into the Palearctic from the Old World tropics, perhaps through some temporary opening in a physiographic barrier, or it may have evolved from a paramyid parent population in the Palearctic Region. There some chance combination of genetic makeup and possibly the crowded condition of other rodent niches must have enabled and required it gradually to evolve a habit of seeking food in the trees. The arboreal niche may have been empty or already occupied by other species which it was necessary for the new species to replace.

The ancestral species of diurnal squirrels (or some species ancestral to it?) thus made progress in adaptation to going up into trees to obtain the fruit, for the natural falling of which other rodents would be obliged to wait. Foraging in the trees may considerably extend the period of support derived from some important tree foods. For example, on the southeastern coastal plain of North America the tree squirrel, *Sciurus niger,* begins to climb the long-leaf pine in early June to cut its cones and feed on the unripe seed, but terrestrial rodents must utilize some other food supply until November (Moore, 1957, p. 10) when the cones begin to open and let the ripe seed fall. It is interesting that Broadbooks (1958, p. 24) observed the chipmunk species *Eutamias amoenus* forage for ripening seed in the highest western yellow pines (*Pinus ponderosa*) and Douglas firs (*Pseudotsuga taxifolia*), before seed had fallen, and on the ground afterward. But concurrently Broadbooks observed that the larger but rather chipmunk-like ground squirrel [*Spermophilus*] *lateralis,* which is sympatric with *E. amoenus* and apparently occupies in many other respects the same niche, did not climb to forage in the trees but fed on the conifer seed when it had fallen.

The habit of climbing trees to escape enemies probably soon followed

adaptation to arboreal foraging. Arboreal nesting may have come next. Even more distinctive among the adaptations of the subfamily of diurnal squirrels is its adjustment to diurnal activity. Diurnality may have been made possible by the greater safety from terrestrial predators that is attained by foraging, refuge seeking, and nesting in the trees.

One Possible Hypothetical History

When the enormous expanse of coniferous and deciduous forests in the Palearctic first became available to the first tree-foraging species as a single-species range, the species probably entered upon a period of accelerated accumulation of favorable mutations and became able to spread into less favorable habitats. Populations of this improved species must have occasionally spread through filter barriers, become isolated in forested regions beyond the barriers, and speciated. After some subsequent history, about which the living Sciurinae seem to tell us nothing, the dominant tree-squirrel species might have had three pairs of transbullar septa and produced some of the phyla still living today, including the genus *Tamiasciurus* in the Nearctic Region. The character of having two septa may have evolved later and species possessing it may have replaced, to a great extent, the forms with three septa. Holarctic descendants, which are dominant at the present time, all have two pairs of transbullar septa (Moore, 1959).

At some period when the Bering Isthmus became habitable by tree squirrels, a population spread across it into the Nearctic Region and subsequently became isolated there. Perhaps encountering competition from other species of tree squirrels, which may have originated in a similar manner before it, this newly forming species survived through the chance possession of characters that enabled it to regress successfully to somewhat terrestrial habits but to retain the characteristic of diurnal activity. Later the newly established phylum of Nearctic ground squirrels became locally dominant in this niche, perhaps, but not necessarily, radiated in the Nearctic, and spread back across the Bering Isthmus. By the time of recrossing the Bering land bridge, however, it must have been so differentiated in habits as not to enter into competition with the dominant Palearctic species of tree squirrel. Presumably upon becoming isolated in the Palearctic Region, speciating, and acquiring a vast Palearctic range, this chipmunk improved its adaptations and became a dominant species.

Populations of this Palearctic, dominant, but generalized species of chipmunk, *Eutamias sibiricus,* spreading eastward across the Bering land bridge during periods of favorable conditions may have in time given

rise to many Nearctic species. Eventually, one of these adapted better to open meadows and prairies than to brushlands and forest edges, so that it avoided competing with either chipmunks or tree squirrels and could thrive while sympatric with them. Quite possibly it then radiated and originated a new phylum. The successful spread of the newer phylum of ground squirrels, the Spermophilina, to the Palearctic Region would eventually enable it to speciate there. The newest Holarctic squirrel phylum probably evolved then as a dominant species in the Palearctic Region itself. The same process could then have been repeated yet again in the evolution of the phylum of giant ground squirrels, the Marmotina.

The above hypothetical account attempts to show how the potentially greatest range in the world for a single squirrel species may have functioned as a center of dispersal and the Bering Strait and land bridge may have functioned as an isolating mechanism, both important in the evolution of diurnal squirrels (and possibly many other forms of terrestrial vertebrates). For narrative simplicity it had to be written one way. The original species of tree squirrels could quite as well have originated in the Nearctic Region or Old World tropics and later spread to the Palearctic. The point is that once the enormous potential species range on the Palearctic side became occupied for the niche of any particular phylum, the spreading by that phylum across a Bering land bridge from that time onward almost certainly was eastward. Even in the case of more distantly related taxa, such as *Sciurus vulgaris* and *Tamiasciurus hudsonicus* (tribally distinct but evidently occupying the same niche), spreading has evidently been from west to east. For the most part only when a form has evolved in the Nearctic to the extent that it becomes adapted to a niche not occupied in the Palearctic is a spreading likely to proceed from east to west. The exceptions to this thesis would necessarily be species that, by whatever other means, happen to overcome the evolutionary advantage of the great Palearctic species range. If the assumptions made are valid, the place of origin for the three phyla Tamiina, Spermophilina, and Marmotina may well be Nearctic.

SUMMARY

There are four living phyla of diurnal squirrels with taxa on opposite sides of Bering Strait which are differentiated to a degree that is recognized to be of less than generic rank. For each of these four phyla the greatest range of a single species occupies the principal continuous land mass west of the Strait. Also, for each phylum a greater number of species occurs on the east than on the west. It is suggested that, other things being equal, a species that occupies the large Palearctic range is the dom-

inant species in its phylum, and, when ecological conditions are suitable for a spread across the Bering land bridge, it would be the dominant species that would spread. Some of the more numerous Nearctic species are considered to have evolved from the populations that spread from west to east and then to have become geographically isolated. The Palearctic Region is regarded therefore as the center of dispersal for these diurnal squirrel phyla: the subtribes Sciurina, Tamiina, Spermophilina, and Marmotina. The probable place of origin is shown to be the Nearctic Region for the Tamiina, the Spermophilina, and the Marmotina. The large, relatively unbroken area of the northern Palearctic Region is, and may for a long time have been, the largest area available in the world as a range for a single species of terrestrial vertebrates, and the possibility is noted that it may be the area on which the dominant species are evolved in vertebrate phyla other than diurnal squirrels. If such is the case, the above-described mechanism may be conceded to have contributed importantly to the predominantly eastward spreading across the Bering land bridge recognized by Simpson (1947) and Darlington (1957).

Central America, or parts of it, as an island or archipelago must have served as a staging area for the adaptation of squirrel species of Nearctic origin to tropical conditions over perhaps a substantial portion of the Pliocene before the emergence of a Panamanian land bridge gave them access to South America at the end of the Pliocene.

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